30. On the Structure of the Enamel in the Primates and some other Mammals. By J. Thornton Carter, Hon. Research Assistant, University College, University of London.

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(Plates I. to VII.*)

During the past forty years the theory of the evolution of the crowns of mammalian molar teeth, which is associated with the names of Cope and of Osborn, has attracted the attention of a large number of workers, so that a voluminous literature on the subject has accumulated.

Whilst so much work has been devoted to the gross forms of the teeth, it is surprising to find that little attention has been given to the minute anatomy of the dental tissues as evidence in throwing light on the problem of affinity.

In the year 1850, Sir John Tomes, F.R.S., submitted to the Royal Society a contribution, entitled "The Structure of the Dental Tissues of the Order Rodentia" (Phil. Trans. 1850), in which he gave a detailed description of the pattern of the enamel in various genera, and from their comparison drew the interesting conclusion that the various families of Rodents possess a "constant and exclusive character in the structure of the enamel"; further, that there is a "different and distinct character in each of the larger groups, and that the variety of structure is constant throughout members of the same group: we may take, for example, the Sciuridæ, the Muridæ, and the Hystricidæ, in each of which the structure of the enamel is different and in each is highly distinctive" . . . . . . "the varieties in the structure of the dental tissue, with a few isolated exceptions, justify and accord with the arrangements of the order into the several divisions proposed by Mr. Waterhouse and deduced by him from the relations of the several parts of the skull."

Yet a year earlier than the publication of his observations on the histology of the enamel in Rodents, Tomes had contributed to the Philosophical Transactions a paper "On the Dental Tissues in Marsupial Animals" (Phil. Trans. 1849, vol. cxxxix.), in which he demonstrated a marked feature in their enamel in the form of a system of tubes continuous with the dentinal tubes, this being a constant character of the teeth of all Marsupials, excepting only those of the Wombat. This character "attains its utmost development in the Macropodidæ, and is more feebly present in some Dasyuridæ, whilst in *Myrmecobius* and yet further in

* For explanation of the Plates, see p. 607.

Tarsipes it is reduced to small limits" (Tomes, Dental Anatomy, p. 43).

The significance and value of these contributions lies in the fact that Tomes demonstrated clearly that the enamel pattern in Rodents provides a specific criterion of affinity, and that the structure of the enamel in Marsupials, taken in conjunction with other anatomical characters, may be employed to demonstrate Marsupial relationship.

Seventy years have passed since the publication of these researches, but, in so far as I am aware, during that period no one has extended Tomes's work and published the results of the examination of the enamel structure in all the representative members of a diversified order; and further, with the exception of Sir Charles Tomes, F.R.S., the distinguished son of a distinguished father, no one has applied the results obtained to the determination of affinities or relationship in the case of extinct mammals. In a paper on the "Minute Structure of the Teeth of Creodonts, with special reference to their suggested resemblace to Marsupials" (P. Z. S. 1906), Sir C. Tomes employed the character of tubular enamel as a test of Marsupial relationship, and found that in none of the Creodont teeth which he examined was this character present. Included with this Creodont material was a portion of a tooth of *Borhyæna*, one of the Sparassodonta, in the enamel of which Tomes found no trace of tubes. But the Marsupial characters of this group were so numerous that Prof. D. M. S. Watson, F.R.S., asked me to undertake a further examination of the enamel in other members of the suborder, and I was fortunate enough to discover this Marsupial character in the teeth of *Cladosictis*, *Pharsophorus*, and of *Borhyæna* (Journ. Anat. 1919).

Following the provision of the material for the examination of Sparassodont teeth, the authorities of the American Museum of Natural History handed over to me a rich and representative collection of teeth and jaws of Eocene mammals, comprising some eighty genera, which had been formed for the purpose of obtaining a set of sections with the hope that, in the words of Dr. Matthew, "the investigation thereof will provide a new line of evidence for the affinities of mammals, as distinct from the skeleton or the teeth or the soft anatomy" . . . . . and to "have a cross check on relations of the same kind as the cross check between teeth adaptations and feet adaptations." Already several hundreds of sections have been prepared from this material, and the results obtained encourage the hope that Dr. Mathew's expectations will be fulfilled. To obtain the utmost value from such a collection, it is desirable to possess a complete series of sections of teeth of every genus of existing mammalia, and, in consequence, I have laboured to build up a collection of ground sections which should embrace not only representatives of each genus, but also, in so far as is possible, sections of each tooth in the individual dentition.

Included in the material supplied by the American Museum are teeth of Eocene Primates and Menotyphla: this material was found to be highly fossilized and very friable, and before examining it thoroughly, I decided to complete my collection of tooth sections of recent Primates. A large number of old-world and new-world monkeys have been examined, and some 200 sections have been prepared from teeth of practically all the members of the suborder Lemuroidea.

The results obtained from this microscopical examination disclose certain new features, which, taken in conjunction with other anatomical characters, should be of value.

The first striking feature to be recorded is that throughout the whole suborder Lemuroidea a constant feature in the enamel is a regular system of tubes continuous with the dentinal tubes. *Chiromys* provides a solitary exception, and thus occupies a position similar to *Phascolomys* amongst the Marsupials. The richness of penetration varies greatly both in the teeth of different families and also in different areas of the enamel of individual teeth *.

In the Lemuriformes the amount of penetration is usually slight, seldom exceeding the extent shown in Pl. II. fig. 2, where the tubes (*t*) are seen to pass through about half the thickness of the enamel: over the apex of the unworn incisor teeth and in the cusps of the molars the tubes often pass outwards to within a short distance of the free surface, as shown in Pl. III. fig. 2. As one passes downwards towards the neck of the tooth and the enamel becomes thinner, the penetration becomes more sparse, most of the dentinal tubes splitting up into a fine brushwork just beneath the enamel surface. Such tubes as pass over into the enamel traverse a layer of uncalcified tissue shown in Pl. II. figs. 1 & 2 and designated by the letters *u.l.*

In the Indrisinæ the tubular penetration is extremely rich, rivalling the extent found in the Macropodidæ; for over the apices of the cusps of all the teeth there are tubes in the enamel continuous with almost every dentinal tube, and these pass outwards through the greater thickness of the enamel. The illustrations shown in Pl. I. figs. 1 & 2 give a clearer idea of this condition than can be conveyed by a verbal description.

Towards the necks of the teeth the penetration is still quite rich, but in the sulcuses of the crowns of the molars the penetration does not proceed to any great extent.

In *Propithecus* the degree of penetration is markedly less than in the Indrisinæ, but in certain areas of the enamel it is a conspicuous feature (Pl. II. fig. 3).

In the Lorisidæ there is a very rich penetration, attaining its

* For simplicity I retain the terms "tube" and "penetration," since they are employed in all text-books in the description of this condition in the enamel, but I consider the so-called tubes to be fibrils, epiblastic in origin, and though continuous with the dentinal fibrils, they are not a penetration of these structures into the enamel (*vide* Carter, Phil. Trans. Roy. Soc. ser. B, ccviii. 1917).

greatest development in the enamel of the tooth-cusps. With a view to economy of illustration, I have not included a photo-micrograph of their enamel, resembling as it does the enamel of the Galagos, illustrated in Pl. III. fig. 3.

In *Perodicticus potto* (Pl. VI. fig. 4) the penetration is not nearly so rich as in the Lorises and the Galagos, whilst in *Nycticebus* (Pl. VI. fig. 3) it is but slight, many of the tubes in the enamel of the molars ending just within the enamel in the form of small bulbous spindles similar to those shown in the enamel of *Callithrix* (Pl. IV. fig. 3).

In *Tarsius*, concerning whose position in the classification of the Primates so much has been written in recent years, the penetration attains a degree of richness even greater than is found in the enamel of *Galago*, and rivals in extent the condition shown in *Indris* (Pl. III. fig. 1).

The actual structure of the enamel in the Lemurs also presents features of great interest, inasmuch as one finds that in sections of the entire tooth, the general pattern, or form and arrangement of the prisms, in the Asian and African forms differs from that of the Mascarene Lemurs, and that the enamel of *Tarsius* is to all intents and purposes identical with that of *Galago*.

The pattern of the Mascarene genera is shown in the photo-micrograph of a molar of *Indris* (Pl. V. fig. 1), and this pattern is constant for all the genera, including *Chiromys* (Pl. V. fig. 2). Immediately beneath, on the same plate, is a photo-micrograph of a portion of the enamel of *Semnopithecus* (Pl. V. fig. 3), and it will be seen that the general structure is closely similar to the two lemurs, the enamel being composed of prisms or rods of a somewhat granular structure and with straight, even margins, the prisms being separated one from another by a slight amount of calcified interstitial substance.

The enamel pattern in the Asian and African Lemurs is quite distinct from that seen in the Mascarene forms. It is composed of rods or prisms with undulating margins, which in longitudinal section present a sharply-defined picture showing the wavy outline of the margins of the rods (Pl. IV. fig. 1). In transverse section (Pl. VI. fig. 2) these are seen to be cylindrical rods (*e.r.*), separated one from another by a considerable amount of the calcified interstitial substance usually designated by workers on the histology of enamel as the interprismatic material (*i.p.m.*).

A pattern of enamel identical with this obtains in the teeth of the Hapalidæ and the Cebidæ. In *Callithrix*, which Gregory regards as a very primitive form, there is a slight degree of penetration of the enamel, the prolongation of the dentinal tubes terminating in the enamel (*e*) in the form of little bulbous spindles (*b*) (Pl. IV. fig. 3). The close similarity of the enamel pattern of *Callithrix*, which is identical with that of all other Platyrrhines, to the pattern of *Galago* and of *Tarsius* will be apparent on comparing the micro-photographs figured (Pl. IV.).

I have prepared sections of teeth of *Megaladapis grandidieri* and of *Palæopropithecus* from the Pleistocene of Madagascar. In the former penetration was almost absent, but in *Palæopropithecus* a system of tube is present, developed to an extent which equals the condition seen in the teeth of *Propithecus* itself (Pl. II. fig. 3).

In pattern both forms have an enamel identical with that of the recent Mascarene forms.

The microscopical examination of the enamel in Primates therefore discloses certain features which have not been noted before. They are :—

(1) The enamel in all Lemurs, with the exception of *Chiromys*, possesses a system of tubes continuous with the dentinal tubes. In *Indris* and *Propithecus* the penetration is very rich, but in the Lemurinæ it is feebly developed. In the Galagos, the Lorises, and in *Perodicticus potto* the penetration is rich also, but in *Nycticebus* it is slight, so slight, in fact, that except in the apices of the cusps, the penetration is reduced to a degree which is but little greater than one finds in the teeth of the South American monkeys.

(2) There is a marked and constant difference between the enamel pattern in the Mascarene forms and the Asian and African forms, the enamel in the former having a pattern identical with that found in the Catarrhines, whilst the Asian and African forms present a pattern identical with that seen in the teeth of the Platyrrhines. The Lemuroidea, therefore, parallel the Anthropoidea in enamel structure.

(3) *Tarsius* has an enamel indistinguishable in sections from that of *Galago*.

Amongst living mammals the penetration of the enamel by tubes is, as already stated, a character found in all Marsupials, *Phascolomys* excepted. No other order possesses this character as a constant feature of all its genera.

In the order Insectivora, however, there are a number of genera which do possess it. In the Menotyphla one finds an extremely rich penetration in the enamel of the Macroscelidæ (*Petrodromus* and *Rhyncocyon* were examined), but in sections prepared from a large number of teeth from skulls of *Tupaia* there is no trace of any penetration. In the Lipotyphla all teeth of Soricinæ and of Crocidurinæ have enamel which is richly tubular. *Erinaceus* has a moderate degree of penetration, but *Gymnura* has none. The Talpinæ also do not disclose any penetration.

The two genera comprising the suborder Hyracoidea have an enamel which is richly tubular.

The only other living mammal which possesses this character in the enamel is the Jerboa, one solitary creature out of the large number comprising the order Rodentia.

In the enamel of the teeth of all fossil Marsupials which I have examined, extending back to *Peradectes* (from the Tiffany beds of Colorado (Lower Eocene)), there is a penetration.

In the suborder Multituberculata (Allotheria), which Dr. Matthew tells me he regards as in the Metatherian stage of evolution, but separate from the Marsupials and Placentals, I have also discovered a rich penetration and a distinct pattern of enamel, which will be alluded to later in this communication.

With the presentation of fresh details of the minute anatomy of the teeth the first question to arise is that of their significance.

Is the tubular system of the enamel to be regarded as an heritage derived from remoter ancestors, or has it some adaptive significance in relation to the present needs of its possessor?

To throw light on the question, I have prepared sections of teeth of several primitive Primates.

In the enamel of *Notharctus* and of *Pelycodus*, undoubted Lemuroid Primates from the Lower Eocene, I have been able to discover no trace of penetration by tubes, although I have prepared a number of sections from teeth of different specimens.

In *Hemiacodon*, one of the Anaptomorphidæ from the Middle Eocene, there is marked penetration, well shown in Pl. VI. fig. 1, where, in the enamel over the apex of the tooth, the tubes (*t*) are clearly shown passing some distance into the enamel, though a little further down in the crown of the same tooth all trace of structure, in both enamel and in dentine, had become obliterated in the process of fossilization.

In *Phenacolemur*, concerning whose affinities there has been some discussion (Broili and Schlosser including it amongst the Insectivores, whilst Dr. Matthew, in his list of Eocene material supplied to me, includes it amongst the Menotyphla), the enamel is also tubular.

Nothodectes (*Plesiadapis*), whose affinities also are doubtful, discloses no sign of penetration, and the structure of its enamel lends no support to the views of Stehlin that it is closely akin to the Chiromyidæ, but rather supports the opinion of Matthew that it is nearer to the Menotyphla, and is a primitive synthetic type intermediate between Tupaiaoids and Lemuroids.

With regard to the microstructure of the enamel in these extinct Primates, it is interesting to record that *Hemiacodon* possessed an enamel identical in pattern with that of *Tarsius* of the Asian and African Lemurs, and therefore with that of the Platyrrhinæ, whilst *Notharctus* and its forerunners *Pelycodus* disclose a structure similar to that found in the Mascarene forms, living and extinct, and to the Catarrhinæ.

It is obvious, therefore, that, in the examination of a fragment of a tooth, the discovery of the presence of a system of tubes in the enamel, unsupported by other evidence, would not afford a precise test of affinity; but, taken in conjunction with the pattern of the enamel, the demonstration of tubes would enable one to state, with a degree of certainty, as to whether such a fragment had been derived from a Multituberculate, a Marsupial, an Insectivore, a Lemur, or whether the tooth was that of a Jerboa; and further, as the evidence adduced in this paper shows, in the case of a Lemur one could differentiate between the Mascarene and the Asian and African forms.

It remains for me to give a very brief description in general of the tubular enamels of those mammals apart from the Lemurs to which I have alluded.

The enamel pattern of the Multituberculates is quite distinctive, and differs fundamentally from all others which I have examined. If a section of a tooth of *Polymastodon* be ground and examined (Pl. VII. fig. 5), tubes (*t*) will be seen passing from the dentine (*d*) into the enamel (*e*): by careful illumination a faint pattern may be discerned, which can be developed by washing the section for a time in acid alcohol until such an image as is shown in Pl. VII. figs. 2, 3, and 4 is disclosed.

Here one sees a series of horseshoe-shaped bodies (*h.s.*), which become smaller and more widely separated as the outer edge of the enamel is approached. In whatever plane the section may be cut these structures never become complete circles, the two ends remaining apart and terminating in bulbous slightly recurved enlargements. Such an image would be seen in transverse section of any spiral structure.

Any further description of the minute structure of this peculiar enamel would be out of place in this paper, but it may be mentioned that *Ptilodus* also has an enamel which is richly tubular and an enamel pattern similar to, but by no means identical with, that of *Polymastodon*.

The Marsupials possess a very distinctive general pattern, as is shown in Pl. VII. fig. 1, where the rods or prisms (*p*) are seen, in transverse section, to be arranged in rows which sometimes merge: these rows are separated by a very definite area of interprismatic material (*i.p.m.*), so that, as Dr. Mummery has pointed out, in teased preparations of developing enamel this substance splits up into laminæ. The dark dots (*t*) are the so-called tubes seen in section. A section showing the enamel prisms in such rows and presenting the tube-penetration is peculiar to Marsupials.

I have not figured the richly tubular enamal of the Jerboa, but it is the only rodent which shows any trace of tube-penetration, and its enamel pattern presents the criss-cross arrangement of the rods which Sir John Tomes showed to be a character peculiar to the Rodents.

With regard to the significance of the presence of a system of tubes in the enamel, the variability of its degree and of its distribution and the fact that, whilst richly developed in one creature it may be totally absent in a closely-related form, would seem to indicate that it is connected with some adaptive process, and that, taken alone, it has little or no value as evidence of affinity or line of descent.

The microstructure of the enamel, however, appears to be particularly constant. In the long and well-authenticated series of creatures comprising the ancestry of the Horses, the microstructure of the enamel does not change, in spite of the modification of the teeth from the brachydont form in *Eohippus* through all the progressive stages leading up to the complex hypsodont molar teeth of recent horses.

In the Marsupials the pattern of the enamel in recent and fossil Australian forms appears to be identical with that of the teeth of *Peradectes* from the Tiffany beds of Colorado (Lower Eocene).

Certain fossil rodents from the Eocene exhibit a close similarity in enamel structure to recent forms, and where, as in *Chiromys*, a Lemur has evolved a rodent dentition, the structure of its enamel still retains its Lemurine character.

It was my intention to hold over a description of the minute structure of the teeth of Primates until I had published an account of the structure of the teeth in Insectivores, recent and fossil, and of the primitive Creodonts, the material for which has been examined, together with that of a large number of other Eocene mammals. But Professor J. P. Hill, F.R.S., and Professor D. M. S. Watson, F.R.S., were of the opinion that the facts presented in this communication would be of immediate interest to the Fellows of the Society, the more so as recent palæontological discoveries have provided fresh evidence of the antiquity of the Higher Primates.

In conclusion, I have to express my deep gratitude to my colleague, Major G. S. Sansom, and to Mr. F. J. Pittock for their kindness in preparing the micro-photographs used in the illustrations, and to Professors Hill and Watson for constant encouragement.

Above all I have to thank Dr. W. D. Matthew, F.R.S., for providing invaluable material, and for most valuable information and suggestion in conversation during his recent visit to Europe.

Most of the recent material employed was acquired by purchase, but I am deeply indebted to the Zoological Society through Mr. R. I. Pocock, F.R.S., for the gift of teeth of *Chiromys*, and to Professor J. Elliot Smith, F.R.S., for a mandible of *Tarsius*.

Summary.

A microscopical examination of the teeth of Primates discloses the fact that all members of the suborder Lemuroidea possess, in a varying extent, the character of a penetration of tubes into the enamel.

In the Lemurinæ this penetration is slight, but in the Indrisinæ it is very rich.

The Galagos and Pottos also have a rich penetration, but in *Nycticebus* it is but feeble.

Tarsius has an enamel richly tubular, and in its structure essentially Lemurine.

A further interesting feature is that the pattern of the enamel in the Mascarene Lemurs differs from that of the Asian and African forms, and that the former has a structure identical with that found in the enamel of all Catarrhines, whilst the structure of the enamel in the Platyrrhines is identical with that found in the Asian and African Lemurs.

Two primitive Lemuroid Primates, *Pelycodus* and *Notharctus*, from the Eocene show no penetration, but in the structure of their enamel resemble the Mascarene Lemurs.

Hemiacodon, a Tarsioid Primate, also from the Eocene, has an enamel which is tubular, and in structure appears identical with the enamel of the recent *Tarsius*.

The enamel pattern affords a useful test of affinity if taken in conjunction with the character of a tube-penetration, and enables one to discriminate between Multituberculates, Marsupials, and Placentals.

EXPLANATION OF THE PLATES.

The following is a list of reference letters common to the various figures :—

b. bulbous spindles.
d. dentine.
e. enamel.
e.r. enamel rods.
h.s. horseshoe-shaped bodies.
i.p.m. interprismatic material.
u.l. uncalcified layer.

Plate I.

Fig. 1. Longitudinal section through the incisor of *Indris*, showing the presence in the enamel (*e*) of tubes (*t*) continuous with those of the dentine. × 180.

Fig. 2. Longitudinal section through the protocone of an upper molar of *Indris*, showing a similar condition to that seen in fig. 1. × 180.

Plate II.

Fig. 1. Longitudinal section of a lower incisor of *Lemur catta*, showing the form and structure of the enamel rods or prisms (*p*), and at the surface of the dentine (*d*) next the enamel a layer of uncalcified material (*u.l.*). × 350.

Fig. 2. Longitudinal section of a lower incisor of *Lemur*, showing the passage of tubes (*t*) from the dentine (*d*) into the enamel (*e*); the tubes traversing the layer of uncalcified material (*u.l.*) are shown in fig. 1. × 350.

Fig. 3. Section of a lower premolar of *Propithecus*, showing the presence of tubes (*t*) in the enamel (*e*). × 300.

Plate III.

Fig. 1. Section of a tooth of *Tarsius*, showing the junction of the tubes (*t*) in the enamel (*e*) with those of the dentine (*d*). × 450.

Fig. 2. Section of a lower incisor of *Microcebus*. × 250.

Fig. 3. Section from the coronal surface of a lower molar of *Galago*. × 350.

Plate IV.

Fig. 1. Section of a tooth of *Tarsius*, showing the general pattern of the enamel (*e*) with the undulating margins of the enamel rods (*e.r.*) and the tubes (*t*) in the enamel. × 350.

Fig. 2. Section of a tooth of *Galago*, presenting an appearance identical with that shown in fig. 1. × 340.

Fig. 3. Section of a premolar tooth of *Callithrix* (*Callicebus*), showing an enamel pattern similar to *Tarsius* and to *Galago*. The dentinal tubes terminate a very short distance within the enamel as little bulbous spindles (*b*). × 350.

Plate V.

Fig. 1. Section of the occlusal surface of the left upper molar of *Indris*; the photomicrograph taken from the same tooth as the illustration shown in Pl. I. fig. 2. The tubes (*t*) pass but a short distance into the enamel (*e*). The pattern of the enamel is clearly shown, the enamel rods (*e.r.*) having straight margins and showing a fine granular structure. × 450.

Fig. 2. Section of a molar of *Chiromys*. The dentinal tubes terminate at the amelodentinal junction. The pattern of the enamel is similar to that of the other Mascarene Lemurs. × 500.

Fig. 3. Section of enamel of *Semnopithecus*. × 450.

Plate VI.

Fig. 1. Section of a cusp of a molar of *Hemiacodon*, showing the presence of tubes (*t*) in the enamel (*e*). × 275.

Fig. 2. Transverse section of an incisor of *Galago*, showing the enamel rods (*e.r.*) cut across and having a circular form separated one from another by a considerable amount of interprismatic material (*i.p.m.*). × 300.

Fig. 3. Section of a molar of *Nycticebus*, showing the slight amount of penetration of the "tubes" (*t*) into the enamel, whilst many end in a bulbous spindle (*b*) similar to those shown in the enamel of *Callithrix* (Pl. IV. fig. 3). × 300.

Fig. 4. Section of an incisor of *Perodicticus potto*, showing the passage of tubes (*t*) and an enamel pattern identical with that seen in *Galago* and in *Tarsius*. × 340.

Plate VII.

Fig. 1. Section of an incisor of *Macropus ruficollis*, showing the enamel rods (*e.r.*), cut transversely, lying in rows which are separated by sharply-defined areas of interprismatic material (*i.p.m.*). The "tubes" of the enamel are seen as black dots (*t*). × 1500.

Fig. 2. A transverse section of the enamel of a molar of *Polymastodon*, etched to show the structure. The horseshoe-shaped bodies with bulbous ends (*h.s.*) would suggest sections through an elongated spiral since they never form complete rings. × 275.

Fig. 3. Transverse section through the enamel of the lower incisor of *Polymastodon*, showing a similar condition to that seen in fig. 2, but demonstrating a finely granular structure of the areas embraced within the horseshoe-shaped bodies. × 400.

Fig. 4. Longitudinal section of the enamel of a molar. × 480.

Fig. 5. Unetched section of a molar of *Polymastodon*, showing the passage of tubes (*t*) from the dentine (*d*) into the enamel (*e*). × 300.